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LIGHT AS A FACTOR IN THE GROWTH AND METABOLISM OF TREE SEEDLINGS

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE

UNIVERSITY OF MINNESOTA

BY

GEORGE PETER STEINBAUER

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF DOCTOR OF PHILOSOPHY

AUGUST, 1929

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FOREWORD

The experimental studies described in the following pages were made possible by the facilities and material assistance furnished by the Division of Botany and Plant Pathology of the Minnesota Experiment Station, the Department of Botany of the University of Minnesota, and the Forest Experiment Station, Cloquet, Minnesota.

The writer wishes to express his sincere appreciation to Dr. R. B. Harvey for his kindly suggestions during the course of the experiments and to all others whose interest and suggestions contributed to the execution of the studies described.

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LIGHT AS A FACTOR IN THE GROWTH AND METABOLISM OF TREE SEEDLINGS

Light or visible radiation constitutes one of the most important factors in the growth and development of plants. Under ordinary conditions the quantity of light available for plant use is far in excess of the light requirements. Other external and internal factors such as temperature, carbon dioxide concentration and humidity of the air and the chlorophyll content of the leaves may limit the photosynthetic process long before the greatest possible amount of light has been used. Light may, however, become a limiting factor in the growth and development of plants growing within a forest environment due to the absorption and reflection of light by the tree crowns. The purpose of the present paper is to summarize briefly the physiological and ecological significance of light as a growth and developmental factor as indicated by previous investigations and to report the results of experiments by the writer on certain phases of the problem.

The influence of light on the development and growth of plants may manifest itself in a multitude of ways. From a physiological viewpoint, however, light is primarily of importance as a source of energy for the conversion of carbon dioxide and water into food materials within the living plant. Approximately from .5% to .6% of the radiant energy falling on a leaf surface is utilized in carbon assimilation. The actual amount varies with the external conditions and the nature of the plant itself. Thus Lundegardh [1] found that while certain shade plants such as Oxalis spp. reach their maximum rate of assimilation of carbon at a light intensity of one-tenth that of full daylight, other plants continued to increase their rate with increased illumination. Brown and Heise [2] state that a review of the literature does not show that carbon assimilation by plants is proportional to light intensity, but that it really indicates a progressively smaller augmentation in the rate as light intensity increases until a point is reached at which no measurable increase is produced by further increase in illumination. Blackman [3] points out, however, that as long as light is the only limiting factor, an increase in illumination yields an increase in assimilatory rate nearly proportional to the increase in light intensity.

Not only does the rate of carbon assimilation vary with the light intensity, but it proceeds at a greater rate in certain parts of the visible

[1] Lundegardh, Henrik. Klima und Boden in ihrer Wirkung auf das Pflanzenleben. Jena 1925.

[2] Brown, W. H., and Heise, G. W. The relation between light intensity and carbon assimilation. Philippine Jour. Sci. Sec. C. *12:* 85-97 (1917).

[3] Blackman, F. F. Optima and limiting factors. Ann. Bot. *19:* 281-295 (1905).

spectrum than in others. The investigations of Kniep and Minder,[4] Timiriazev,[5] and Ursprung [6] indicate that light absorption and carbon assimilation take place in all parts of the visible spectrum and to a limited extent in the infra-red and ultra-violet. The following graph illustrates

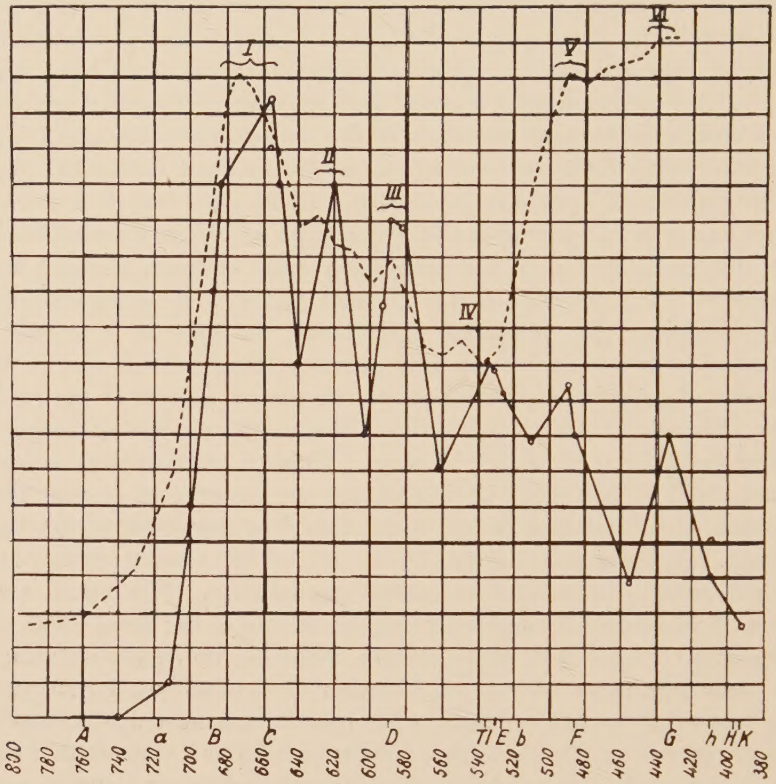

FIG. 1. Graph showing relation between light absorption (broken line) and starch formation (solid line) in the different parts of the spectrum. Roman numerals represent bands of maximum absorption of light. (Ursprung 1918.)

the relation between light absorption and carbon assimilation in the different parts of the spectrum. It will be noted that on the basis of equal energy content the most effective portion of the spectrum lies between the B. and C. Fraunhofer lines.

[4] Kniep, H., and Minder, F. Uber den Einfluss verschiedenfarbigen Lichtes auf die Kohlensaureassimilation. Zeitschr. f. Bot. *1:* 619-650 (1909).

[5] Timiriazev, C. Recherches sur la decomposition de l'acide carbonique dans le spectre solaire, par les parties vertes des vegeteaux. Ann. Chim. et Phys. *12:* 355-396 (1877).

[6] Ursprung, A. Uber die Bedeutung der Wellenlange fur die Starkebildung. Ber. d. Deut. Got. Gesel. *36:* 86-100 (1918).

Light exerts a pronounced influence on the transpiration rate of plants. The light energy is largely converted into heat energy and thus utilized in transpiration. The researches of Lloyd [7] and others indicate that it may have a marked influence on the opening and closing of stomata. The relation between radiation and transpiration is illustrated in Fig. 2. The lag of transpiration behind radiation is probably to be explained as a result of a prolonged rise in temperature even after the intensity of solar radiation has begun to decrease.

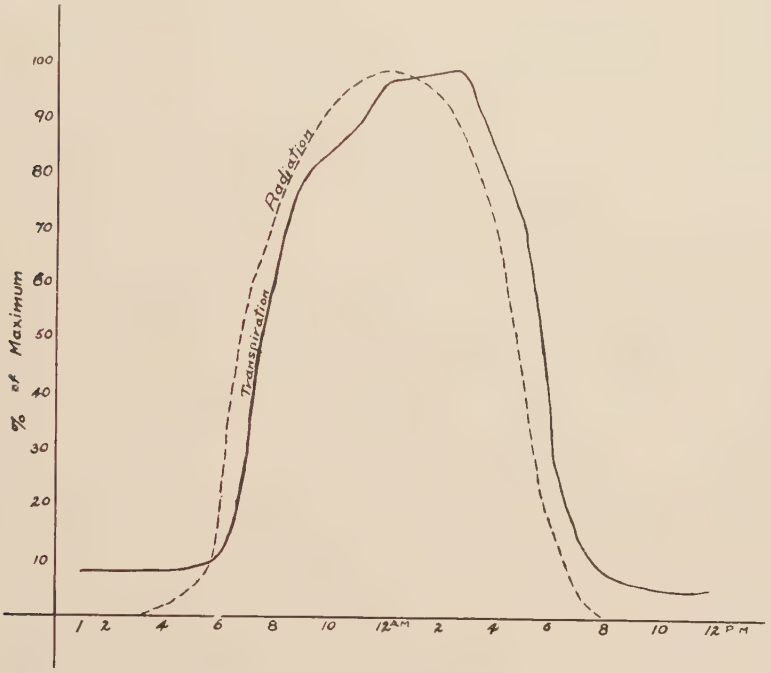

FIG. 2. Graph showing the influence of intensity of solar radiation on the rate of transpiration throughout the day. (Briggs and Shantz[8].)

Although several lower plants and many Gymnosperms are able to form chlorophyll in the absence of light, most Angiosperms cannot do so. Schmidt [9] concludes that the wave lengths of light most strongly absorbed by chlorophyll are also those most effective in its formation. Wiesner [10] has shown that the minimum light intensity required for chlorophyll formation is much lower than that required for assimilation. Willstatter [11] found that the chlorophyll content of shade leaves was usually higher than sun

[7] Lloyd, F. E. The physiology of stomata. Carnegie Inst. Wash. Publication No. 82.

[8] Briggs, L. J. and Shantz, H. L. Hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agr. Res. *5:* 583-649 (1916).

leaves of the same species, indicating that high light intensity may even have a disintegrating effect upon chlorophyll.

Plant growth may be influenced by the intensity, quality, and duration of light. The literature dealing with the morphogenic influence of light and darkness upon plant development has been reviewed in considerable detail by MacDougal.[12] He points out that the distinct effects brought about by changes in light intensity and quality are not easily analyzed. He considers light as a stimulative influence on morphological differentiation and growth and states that every species appears to be attuned to a certain range of intensities of the various environmental factors and capable of carrying out its chief physiologic and morphologic functions only within this range. No satisfactory explanation has yet been given to the phenomena collectively known as "etiolation." The experiments of Godlewski [13] indicate that such conditions are not due solely to cessation of the photosynthetic process since they occurred even when plants were placed in an atmosphere devoid of carbon dioxide.

Certain processes such as flowering and fruiting in plants seem to be controlled by the duration of light to which the plants are subjected. Garner and Allard [14] use the term "photoperiodism" to express the response of plants to differences in the relative length of day and night. They separate plants into three groups: long-, medium-, and short-day plants, depending upon the period of illumination best suited to normal development, growth and reproduction.

Differences in the minimum light requirements of plants are of importance in determining the survival of different species when in competition with one another. This is especially true when they are growing beneath a forest canopy where the light conditions may be considerably different from those in the open. Such terms as "tolerance" and "intolerance" of shade have come into use as expressions of the ability or inability of a plant to reproduce or maintain itself under shade conditions. Foresters and ecologists have constructed scales of tolerance based either upon practical experience or upon growth studies in conjunction with light measurements. The extent to which light itself is the determining factor in plant growth

[9] Schmidt, A. Die Abhangigkeit der Chlorophyllbildung von der Wellenlange des Lichtes. Beitrage Biol. Pflanzen *12:* 269-294 (1914).

[10] Wiesner, J. Der Lichtgenuss der Pflanzen. Leipzig (1907).

[11] Willstatter, R., und Stoll, A. Untersuchungen uber chlorophyll. Berlin (1913).

[12] MacDougal, D. T. The influence of light and darkness upon growth and development. Memoirs New York Botanical Garden Vol. II (1903).

[13] Godlewski, E. Zur Kenntnis der Ursachen der Formanderung etiolierter Pflanzen. Bot. Zeitg. *37:* 81-92 (1879).

[14] Garner, W. W., and Allard, H. A. Flowering and fruiting of plants as controlled by length of day. U. S. Dept. Agric. Yearbook 1920, pp. 377-400.

under forest conditions is difficult to determine due to increased root competition and other disturbing influences.

It is highly desirable when studying plant growth and distribution within a forest environment to have a record of the light conditions as well as other habitat factors such as air temperature, and humidity, and soil factors such as temperature, moisture content and chemical and physical composition. Light is by far the most difficult of the environmental variables to measure. This is due to the variability of sunlight itself and to the difficulties involved in making light measurements.

The methods available for making light measurements are described in some detail by Pulling [15] and will be merely outlined here as a means of comparing their possibilities for use in environmental studies.

Light is generally considered as that type of radiation that is capable of creating a sensation when it falls upon the retina of the human eye. Light may be converted into heat or electrical energy and measured as such. Methods of light measurement based upon this fact are spoken of as radiometric measurements. The greatest value of this type of measurement is that light may be measured in energy units. Radiometric instruments are capable of a high degree of precision when carefully constructed, but are usually too delicate or cumbersome for field use. Burns [16] describes an instrument using a thermopile and sensitive galvanometer which might be used for ecological studies, although it can hardly be considered as portable or convenient. Since the thermopile is sensitive to the infra-red and heat waves as well as the visible radiation, care must be taken to remove all but the visible portion. This is usually done by inserting a water cell or other filter to absorb the heat and infra-red radiations. Glass may be used to absorb the ultra-violet light.

Segelken [17] and Shelford and Kunz [18] report the use of photoelectric cells for ecological purposes. With such devices it is possible to secure constant records, which are highly desirable. So far the photoelectric cells used have had unequal sensitivity in the different parts of the spectrum, although considerable improvement has been made to correct this defect. For most cells the sensitivity is greatest in the ultra-violet and violet and almost nil in the red. This is true especially of the earlier sodium and potassium cells. With rubidium and caesium cells the maximum sensitivity is shifted towards the longer wave lengths.

[15] Pulling, H. E. Sunlight and its measurement. Plant World *22:* 151-171 (1919).

[16] Burns, G. P. Studies in tolerance of New England forest trees. VI. A portable instrument for measuring solar radiation in forests. Vermont Agr. Expt. Sta. Bull. 261, 1-30 (1927).

[17] Segelken, J. G. The determination of light intensity. Ecology *10:* 294-297 (1929).

[18] Shelford, V. E., and Kunz, J. Use of photoelectric cells for light measurement in ecological work. Ecol. *10:* 298-311 (1929).

Use has been made of light-sensitive chemicals as a means of determining light intensity. Certain chemical reactions such as the reduction of silver halides to metallic silver occur much more rapidly in light than in darkness. The degree of darkening produced when a photographic emulsion is exposed to light has been used as an index of light intensity. Wiesner [19] was one of the first to use this method for ecological purposes. The main disadvantages in the use of this method are the difficulty in obtaining uniformity in the material and the greater sensitivity of the emulsions to the shorter wave lengths. Pulling [20] points out that while the reciprocity law governing such reactions holds very exactly when comparing light of equal energy distribution curves it tells little or nothing when these conditions are not fulfilled. Klugh [21] suggests the use of panchromatic emulsions to overcome this difficulty.

Various other chemical reactions have been used as a measure of light intensity, but as a whole they have not proven very satisfactory because of the numerous factors influencing such reactions.

Photometry is essentially a comparison of the illuminations produced by two light sources, one of which is known. Such comparisons measure light not in terms of energy units but in terms of brightness or physiological effect. For many purposes the intensity of illumination produced by a light source may be conveniently used as a means of measuring light, irrespective of the actual energy changes involved. The standard unit of illumination has been defined in various ways, but in all cases it refers to the illumination which a standard light at unit distance will produce upon a perfect diffusing surface placed at right angles to the incident beam of light. Photometric measurements are therefore calculated in terms of such units as foot-candles and meter-candles.

Photometric instruments are selective to the extent that they cannot be used for any region outside of the visible spectrum. For most purposes, however, this is the region most important for plant development.

Numerous forms of photometers have been devised, but the great majority are adapted only to laboratory use where a constant light source is available and there is equipment for calibration from time to time. The Macbeth illuminometer has been used for light measurements and seems to be quite satisfactory for most purposes. Allee [22] and Grasovsky [23] have

[19] Wiesner, J. Der Lichtgenuss der Pflanzen. Leipzig (1907).

[20] Pulling, H. E. Sunlight and its measurement. Plant World *22:* 151-171 (1919).

[21] Klugh, A. B. Ecological photometry and a new instrument for measuring light. Ecology *6:* 203-237 (1925).

[22] Allee, W. C. Measurement of environmental factors in the tropical rain-forest in Panama. Ecology *7:* 273-302 (1926).

[23] Grasovsky, Amihud. Some aspects of light in the forest. Yale Univ. Bull. No. 23 (1929).

used it in ecological studies. The latter writer found that it compared favorably with the thermopiles used by Gast and by Burns, although measuring slightly different portions of the spectrum. The instrument consists of a small electric bulb as a light source connected with a source of current, usually dry cells, and so arranged that the illumination produced may be compared to that of the unknown light source. It possesses this advantage over most photometers that it can be calibrated in the field by the operator without the aid of accessory photometric apparatus.

Factors Influencing the Nature of Sunlight

Sunlight is altered in passing through the atmosphere either by reflection or absorption. The greatest diminution in intensity occurs at low altitudes and locations where there is a large amount of suspended material in the air such as dust particles, water vapor and the like. Absorption and reflection are much more pronounced in the shorter wave lengths, especially blue and violet.

Forest Light, Its Spectral Composition

The question of the composition of forest light is a complicated one but nevertheless one of great importance. Zederbauer [24] was one of the first to note differences in the composition of forest light. He made measurements of the light occurring beneath various tree species and concluded that they utilized the different portions of the spectrum in varying degrees. Thus he found that the more tolerant species absorbed the green and yellow to a greater degree than the others. His methods were somewhat open to criticism in that the spectral quality of the filters used in his photometer was not very sharply defined and the benzene lamp used was limited to a small range of intensities.

Knuchel [25] made spectrophotometric measurements under several types of broad-leaved and coniferous trees. His method was to compare the intensity of the light coming vertically through the tree crowns with the intensity of light furnished by a small electric bulb. The light from the known and unknown light sources was passed through a prism to produce the same spectral quality. Balance in light intensity from the two sources was secured by use of Nicol prisms. He made measurements at the following wave lengths: red, 652 millimicrons; yellow, 589; green, 520; blue, 472; and dark blue, 440. The amount of light beneath the forest canopy was expressed as per cent of diffused sky light. His conclusions were that

[24] Zederbauer, E. Das Lichtbedurfniss der Waldbaume und die Lichtmessungen Methoden. Centralblatt fur das ges. Forstwesen *33:* 325-330 (1907). Abst. For. Quart. *6:* 255-262 (1908).

[25] Knuchel, H. Spectrophotometrische Untersuchungen im Walde. Mitteil. d. Schweiz. Centralanstalt fur das forst. Versuchswesen *11:* 1-94 (1914).

there was a preponderance of yellow and green light beneath the crowns of broad-leaved trees due to the filtering effect of the leaves, but that the light beneath coniferous trees was essentially unaltered in spectral quality. He did not find the differences in the light used by various species of trees such as Zederbauer observed. Unfortunately he measured only the vertical component of the light occurring beneath the tree crowns. The light which plants receive may be side light as well as that coming directly through the leaves or through the openings between them.

Lundegardh,[26] using the photographic method and two filters, one transmitting the red-yellow and the other the blue-violet portions of the spectrum, states that the blue and violet is reduced much more than the red-yellow light beneath the tree crowns.

Using a Nutting Spectrophotometer Klugh [27] obtained values indicating a high proportion of blue light beneath the tree crowns.

Wiesner [28] and others, however, maintain that forest light is essentially the same in composition as that in the open, since much of it comes through the openings between the leaves.

A review of the literature on the subject shows a great discordance in the views concerning the nature of forest light. Spectrophotometric measurements usually require rather elaborate apparatus not suited to field studies. The use of filters placed before light instruments to obtain isolated spectral regions for comparison is justifiable only when there is not too great a difference in the intensity of the light sources. The absorptive capacity of a filter depends entirely upon the concentration of the absorptive material. A filter that may be adequate at a low light intensity may have quite a different transmission value if the light intensity exceeds the absorptive capacity of the filter.

It occurred to the writer that the Macbeth illuminometer might possibly be converted into a spectrophotometer suited to field work. With some modifications the instrument can be made very satisfactory for light quality studies in the forest. In view of the unsatisfactory and conflicting views on the subject of forest light it was considered worthy of further study in the hope of harmonizing, if possible, the different interpretations of previous experimental work.

Description and Use of the Illuminometer

The illuminometer as ordinarily equipped is suited only to the comparison of lights of approximately the same spectral quality. Fig. 3 illus-

[26] Lundegardh, H. Klima und Boden in ihrer Wirkung auf das Pflanzenleben. Jena (1925).

[27] Klugh, A. B. A comparison of certain methods of measuring light for ecological purposes. Ecol. *8:* 415-427 (1927).

[28] Wiesner, J. Der Lichtgenuss der Pflanzen. Leipzig (1907).

trates the cross section of the illuminometer. It consists essentially of a small electric bulb mounted on a movable carriage, which furnishes the standard light source, and a comparison field in the form of a Lummer Brodhun cube. A and B are slots into which neutral filters may be inserted to bring the two light sources to a range that may be conveniently measured on the scale of the instrument. Current for the standard lamp is furnished by batteries located in the controller unit and regulated by a milameter. In ecological work it is not necessary to place a neutral filter in the A position since a light intensity as low as 1 foot-candle can be measured without filters and it is hardly conceivable that intensities of lower value than that would be met with in plant habitats. For reducing the unknown light intensity to that measurable on the scale neutral filters

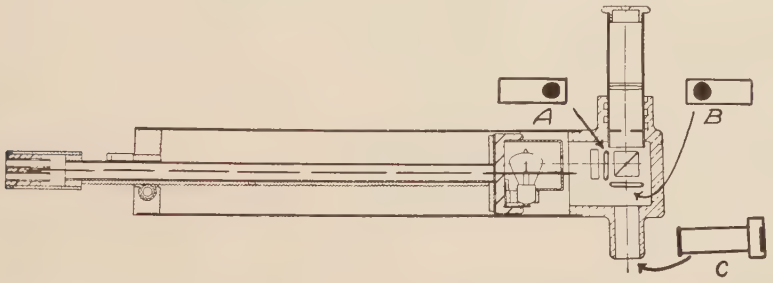

FIG. 3. Cross Section of Illuminometer.

may be inserted in the C position. If color filters of the same transmission values are now inserted in the A and B positions the instrument may be used for determining the light intensity in that portion of the spectrum which the A and B filters transmit.

The objection to the use of filters previously mentioned is eliminated since the instrument requires the use of a neutral filter in the C position if the intensity of the unknown light source becomes greater than 25 foot-candles. In other words, neither spectral filter is at any time exposed to an intensity greater than twenty-five times that of the other.

The choice of filters depends upon the spectral regions to be investigated. Those used in the present study were prepared by inserting in the filter holders strips of gelatin impregnated with dyes of known spectral transmission. The gelatin films were obtained from the Eastman Kodak Company. In a catalog entitled "Wratten Light Filters" there are listed a large number of filters, together with their transmission values determined at intervals of 10 millimicrons upon suitable spectrophotometers. In addition their stability towards sunlight is given. The designation "stable" indicates that there will be no change in transmission if exposed to sunlight for a period of six months. "Moderately stable" means that there may be

a slight change within 3 months. If exposed to light only during measurements they should be light stable almost indefinitely. The filters should be kept in a dry place when not in use. In order to prevent moisture from reaching the gelatin films they may be inserted between two sheets of white celluloid or mica in the filter holders.

The spectral regions selected depend upon the purpose of the measurements. In some cases it is necessary to combine filters to obtain the desired regions. The regions isolated in the present studies were obtained by the use of the following filters: red, 26; yellow, 61 and 22; green, 61 and 44; blue, 48. The transmission values are given in the table below.

TABLE I. PER CENT TRANSMISSION OF FILTERS

Wave Length in Millimicrons	Red 26	Yellow 61, 22	Green 61, 44	Blue 48
400				2.68
410				2.40
420				3.40
430				7.9
440				19.1
450				31.6
460				36.9
470				34.9
480			.98	26.2
490			1.20	17.3
500			7.11	9.1
510			11.99	2.5
520			14.13	
530			11.99	
540			7.66	
550		2.44	3.18	
560		6.01	1.29	
570		7.91		
580		4.46		
590	3.17	1.97		
600	33.1	.62		
610	60.2			
620	74.0			
630	76.0			
640	77.7			
650	79.4			
660	79.4			
670	79.4			
680	79.4			
690	79.4			
700	79.4			

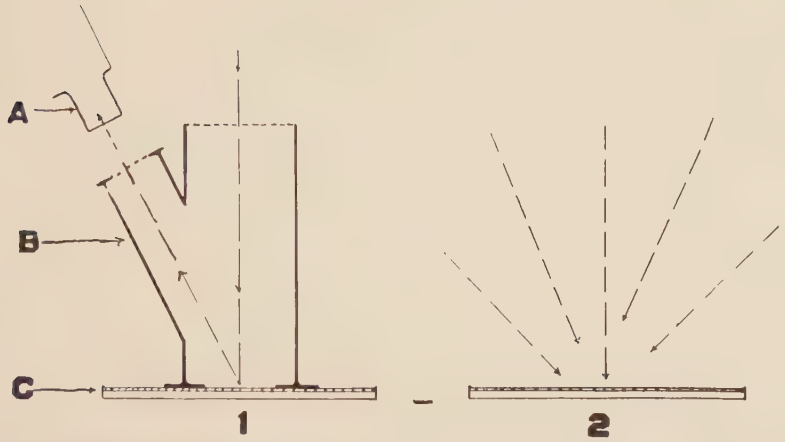

FIG. 4. Diagram showing method of measuring light incident upon test plate from a single direction.

In making measurements in the forest the procedure consists of inserting the spectral filters in the A and B positions and comparing the light from the test plate with that of the standard lamp by moving the standard lamp along the illuminometer tube until a point is reached at which the inner and outer fields are of equal brightness. Matching the two fields is not difficult since the colors used are the same in both filters. The use of a cardboard extension above the eye-piece, so constructed that it fits closely about the eye of the observer, eliminates the eye strain due to distinguishing differences of low light value in the comparison tube when the eye is already adapted to a much higher intensity outside the instrument.

Readings made beneath different types of forest canopy may be compared to the light in the open by removing the test plate to the open and repeating the measurements with the spectral filters. The results of light measurements in the forest may then be expressed as per cent of that light intensity occurring in the open in the different regions of the spectrum studied.

The instrument may also be used to determine the intensity of light that falls upon the test plate from a given direction. This is accomplished by carefully removing the head piece of the reference standard and placing the balance of the reference standard housing on the test plate, thereby allowing only that light to fall upon the plate enclosed in the tube that enters through the opening at the top. Fig. 4 illustrates the use of the test plate and reference standard lamp housing for this purpose. The broken lines indicate the direction of the source of light. A represents the lower end of the head piece of the illuminometer, showing the path of light

reflected from the test plate to the comparison tube. B represents the reference standard lamp housing with lamp removed. C corresponds to the test plate.

The instrument and accessory equipment weighs but fifteen pounds and is compact, therefore permitting it to be readily used for field work.

Experiments and Results of Studies on the Spectral Quality of Forest Light

The purpose of the following series of measurements was to determine the effect of various types of trees upon the light on the forest floor, the direction and source of light under different conditions of shade, and the extent to which light in the shade resembles that transmitted through the leaves of the tree crowns. The determinations were made at the Forest Experiment Station at Cloquet, Minnesota, during the summers of 1927 and 1928 and at the Minnesota Experiment Station during the same period.

The transmission and reflection of light by leaves of a number of species of broad-leaved trees was determined with the Macbeth illuminometer and the four light filters previously described in this paper. Transmission values were determined by measuring the spectral value of light emitted by a frosted 100-watt electric bulb before and after it had passed through the leaf. Measurements of the light value of the light source were made before and after each determination to be sure that there was no fluctuation in intensity during the course of the readings. The values of spectral transmission in terms of per cent of the incident light are averages of measurements on ten leaves of each species and are illustrated in a composite chart in Fig. 5. The small Arabic numbers—1, 2, 3, 4—correspond to the red, yellow, green and blue light filters whose transmission values are given in Table I.

It will be noted that while there are represented in the group species varying widely in tolerance or light requirement the transmission values as a whole show marked similarity. The most striking absorption occurs in the region of the spectrum represented by filter 4 or the blue-violet end of the spectrum. The transmission values in all the species studied were low, in no case exceeding 1 per cent.

The reflective capacity of the leaves of the same species as used in the previous study was also determined. The same light source was used as previously but the light intensity of the bulb was determined by measuring it from the test plate arranged as in Fig. 4, —1. After the value of the light source was thus measured the leaf was inserted between the test plate and the base of the reference standard housing and the light reflected from the leaf determined. The results of determination on six species, ten

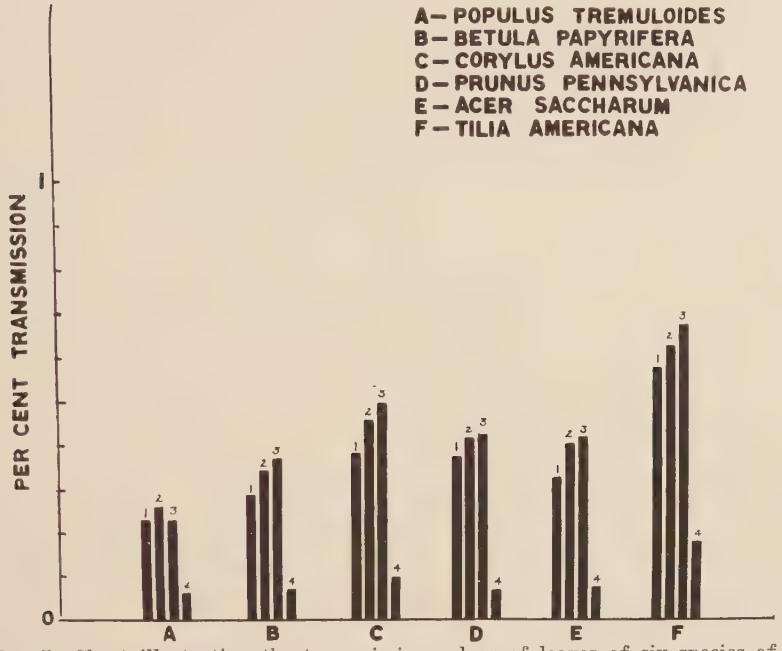

FIG. 5. Chart illustrating the transmission values of leaves of six species of trees.

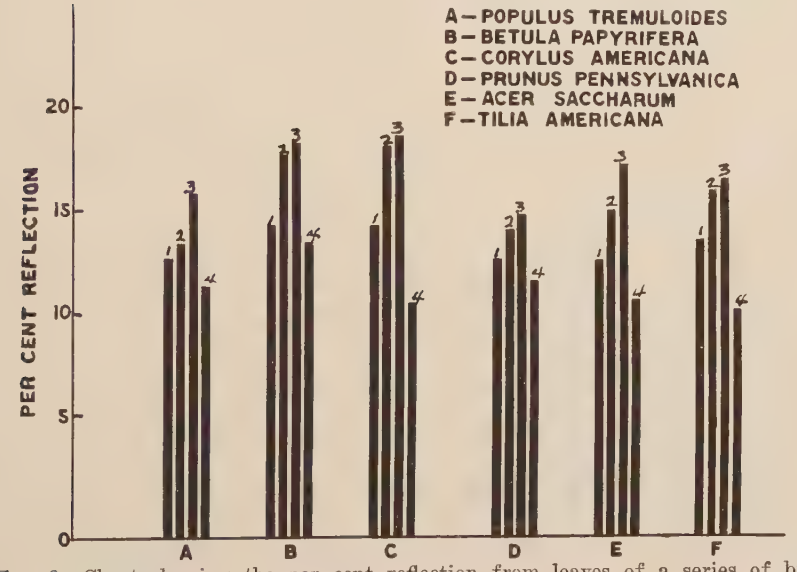

FIG. 6. Chart showing the per cent reflection from leaves of a series of broad-leaved tree species.

leaves of each, are shown in Fig. 6. There is also marked similarity in the reflective power of the leaves of the species studied. Reflection in the different regions of the spectrum varies in a manner similar to that of transmission except that there is less difference between species and between the different portions of the spectrum. The maximum reflection occurs in the region of wave lengths 520-550 millimicrons. Shull[29] working with various leaves and different conditions found the maximum generally in the region of 540-560 millimicrons.

The quality of light found in the shade of forest trees was compared to that found in the open, including both sun light and sky light. All determinations were made on clear days, usually between the hours of 10 a.m. to 2 p.m.

The direction and source of light have been quite generally overlooked in the measurement of forest light. By means of the method previously described it was found possible to obtain a general indication of the direction or source of light under various types of forest canopy. Light available for growth of forest seedlings may be derived from diffused skylight, direct sunlight coming through the openings between the leaves forming what are known as "sun flecks," light transmitted through the leaves, and reflected light from various sources such as foliage and other surfaces. Diffused skylight is relatively rich in the shorter wave lengths which accounts for the blueness of the sky. The relative spectral distribution of sun and sky light in the four regions of the spectrum set off by filters 1, 2, 3, 4, of Table I was determined for a clear day and is illustrated in Fig. 7. The preponderance of shorter wave lengths is evident from the graph.

In order to determine the extent to which light incident upon the test plate in the shade is composed of diffused skylight and of transmitted light, measurements were made of the total light falling upon the plate and that which fell on the plate through the top of the reference standard lamp housing, the latter being placed so that only light coming through the tree crown could reach the test plate. After completing a large number of such determinations under the crowns of broad-leaved and coniferous trees and shrubs such as Corylus, Alnus, and Cornus spp. it became apparent that the spectral quality of light in the shade might be conveniently classified into three types, based upon the amount of light transmitted through the crowns as compared to the total light incident upon the test plate. In the first type, diffused skylight comprises all but a small fraction of the light in the shade. It is found beneath trees having thick crowns such as isolated individuals of Acer saccharum, Tilia americana, and coniferous trees such as Abies balsamea

[29] Shull, C. Reflection of light from the surfaces of leaves. Sci. *67:* 107-108 (1928).

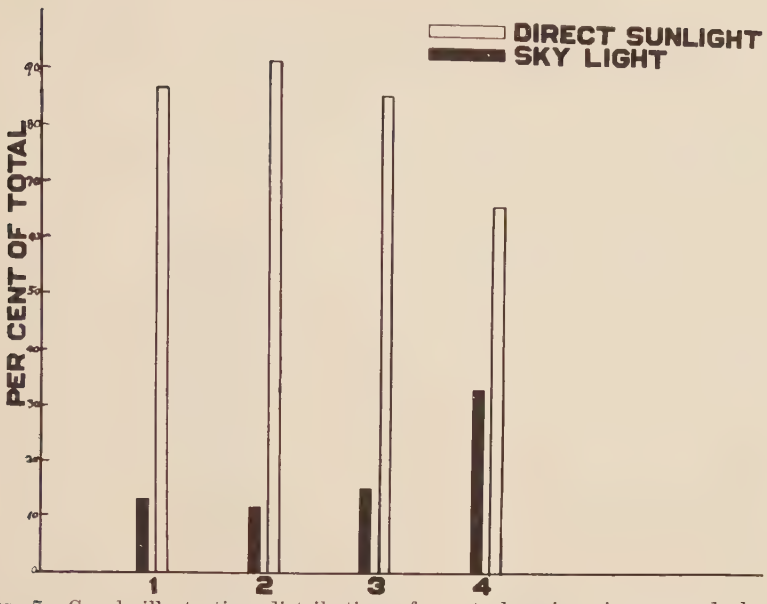

FIG. 7. Graph illustrating distribution of spectral regions in sun and sky light.

and Picea canadensis. The light transmitted by the foliage is almost nil and as a result the spectral quality of the light in the shade does not approximate that transmitted through leaves as illustrated in Fig. 5. On the contrary there is a preponderance of the shorter wave lengths in shade of this type. This is shown in C of Fig. 8 giving the spectral quality of all the light incident upon the test plate when placed beneath an isolated tree of Tilia americana. In the second type sky light, though important, is to a certain extent screened out and as a result there is a falling off in the intensity of the shorter wave lengths and the spectral quality of the light is illustrated in B of Fig. 14. The values illustrated in B were obtained from measurements in a dense stand of trees (Acer saccharum and Tilia americana). The third type forms a shade whose spectral quality resembles that transmitted by leaves. The similarity between C of Fig. 8 and C of Fig. 5 is at once apparent although even in this type the reduction of the intensity of the shorter wave lengths is not as great as in the living leaf. Any canopy that forms more or less of a complete cover, and not included in type I is likely to produce shade of a similar spectral quality to that illustrated in C of Fig. 8. Shade occurring beneath shrubs such as species of Corylus, Cornus, and young growths of Acer saccharum and Tilia americana usually show similar transmission values.

One might conceive that the proportion of shade light that comes directly through the leaves should vary in the above cases and this is

borne out by the following figures obtained from measurements beneath trees and shrubs of the above mentioned three types.

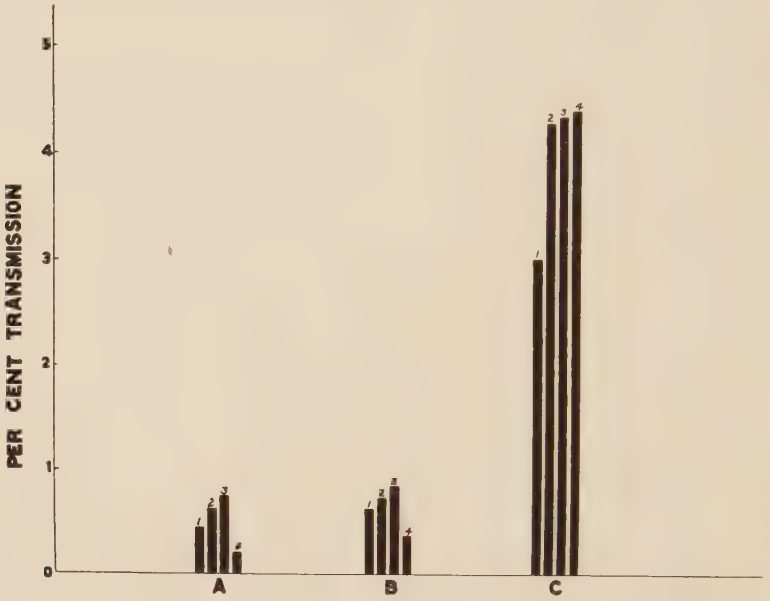

FIG. 8. Graph showing effect of type of leafy canopy on the composition of light in the shade.

TABLE II. EFFECT OF TYPE OF LEAFY CANOPY ON PROPORTION OF LIGHT IN THE SHADE THAT HAS BEEN TRANSMITTED THROUGH LEAVES

Type and Location	Filter	Transmitted Light in % Total Light in Shade
I. Individual ash tree (Fraxinus pennsylvanicum)	1 (Red)	.66%
	2 (Yellow)	.62%
	3 (Green)	.96%
	4 (Blue)	.56%
II. Dense stand of Acer saccharum	1	10.83%
	2	13.07%
	3	13.46%
	4	11.12%
III. Clump of Hazel (Corylus americana)	1	30.71%
	2	23.28%
	3	16.00%
	4	17.64%

It is obvious that little or none of the light is transmitted directly through the leaves in Type I. Light in the shade is composed almost exclusively of sky light. In Types II and III the amount of transmitted light becomes more important and sky light less important as constituents of the total light in the shade. A few illustrations of trees and shrubs occurring in each of the groups are given in the following table:

TABLE III. SPECTRAL COMPOSITION OF LIGHT OCCURRING BENEATH VARIOUS TYPES OF LEAFY CANOPY

Class and Description	Filter	Shade light as % of light in open
I. Picea mariana		
Height, 25 ft.	1 (Red)	2.36%
	2 (Yellow)	1.90%
	3 (Green)	3.21%
	4 (Blue)	3.69%
Abies balsamea,		
young trees, very dense	1	.32%
	2	.22%
	3	.35%
	4	.44%
I. Betula papyrifera,		
individual tree; height, 25 ft.	1	4.45%
	2	3.50%
	3	5.00%
	4	7.07%
I. Pinus strobus		
Height, 80 ft.	1	1.69%
	2	1.62%
	3	2.13%
	4	2.25%
I. Pinus resinosa		
Height, 60 ft., group	1	5.80%
	2	8.27%
	3	8.86%
	4	10.50%

Class and Description	Filter	Shade Per Cent Total Light
II. Betula papyrifera, group 9 trees in 30 sq. yds.; height, 20 ft.	1	.73%
	2	.68%
	3	1.08%
	4	.77%
II. Betula lutea, age 100-120 yrs.; height, 80 ft.; 20 trees per acre	1	1.30%
	2	1.36%
	3	1.42%
	4	.57%
II. Alnus incana, height, 15 ft.	1	.83%
	2	.84%
	3	1.19%
	4	.73%
III. Corylus americana, 15 sprouts per sq. m.; 5-6 ft. tall	1	.49%
	2	.46%
	3	.57%
	4	.19%
III. Acer saccharum, saplings, 8-10 ft.	1	.21%
	2	.29%
	3	.33%
	4	.12%
III. Acer saccharum, height, 40 ft.; age, 40 yrs.	1	.21%
	2	.37%
	3	.37%
	4	.13%
III. Tilia americana, height, 40 ft., surrounded by Acer saccharum	1	.33%
	2	.33%
	3	.46%
	4	.17%
III. Acer saccharum, saplings, 15-20 ft.	1	.27%
	2	.28%
	3	.36%
	4	.14%

After analyzing the above data it is easy to conceive how conflicting opinions regarding the quality of light occurring beneath tree crowns might arise if measurements were taken under different conditions. Basing his opinion on measurements made under spruce and cedar trees Klugh [30] considers forest light to be of essentially a "bluish" nature. On the basis of the data presented by the writer light quality measurements made under the above conditions. would be expected to yield results indicating a preponderance of shorter wave lengths since under the conditions of the measurements the light would be very largely composed of sky light. If, however, the measurements had been taken in a forest composed of Acer saccharum or Tilia americana the opposite conclusion might be arrived at since under such conditions there is a greater reduction in the shorter wave lengths than in the other portions of the spectrum.

Zederbauer's observation that intolerant species utilize less of the green and yellow portions of the spectrum than the more tolerant species is probably to be accounted for by the differences in crown density. Living foliage leaves absorb light in all portions of the visible spectrum although the strongest absorption is in the blue and red portions. When light passes through a very thin leaf or a dilute solution of leaf pigments absorption bands occur first in the blue and red ends of the spectrum. When the light passes through a sufficiently large number of leaves such as in a dense tree crown even the green is absorbed. Intolerant species are generally characterized by relatively open crowns and tolerant species by dense or closed crowns. If determinations of light quality are made under crowns of tolerant and intolerant trees the conclusion that the tolerant species utilize more of the green may at first seem justified. A comparison of the light absorbed by the leaves of trees varying widely in light requirement, however, does not show marked differences in the absorption in the different parts of the spectrum. The data presented in this paper support, in the main, the conclusion reached by Knuchel that shade beneath broad-leaved trees is composed of light relatively rich in green and yellow. There are some exceptions to be noted, however. When side light is taken into consideration it becomes apparent that in some cases already mentioned light transmitted through the crowns is of little consequence in determining the composition of shade light.

The importance of "sun-flecks" must also be considered. In the shade of trees characterized by more or less open crowns such as Populus tremuloides, Pinus banksiana, and many species of Salix the occurrence of sun-flecks is so common that the light occurring beneath the crowns is essentially of the same composition as that in the open.

[30] Klugh, A. B. A comparison of certain methods of measuring light for ecological purposes. Ecol. *8:* 415-427 (1927).

In summary it must be stated that generalizations concerning the spectral quality of forest light are unsafe unless one considers all of the different factors involved. Data based on a few observations under a particular type of tree crown may lead to entirely erroneous conclusions. While there are many factors to be considered the writer has attempted to point out the most important ones that must be taken into consideration.

Effect of Light and Mineral Nutrients on the Growth and Development of Tree Seedlings

The importance of available mineral nutrients upon the tolerance of trees has been emphasized by Lundegardh [31] who points out that the presence of abundant mineral nutrients in the soil favors chlorophyll and foliage formation and thus increases the assimilative capacity of plants under shade conditions. Experimental work on the effect of mineral nutrients on plants grown at low light intensities is lacking, however. The following group of experiments was carried out to determine the effects of concentration of mineral nutrients on tree seedlings grown at or near the minimum light intensity required for growth.

Seedlings of Fraxinus pennsylvanica were germinated in quartz sand and at the age of thirty days transferred to nutrient solutions of various concentrations. The solution used was a three salt solution, consisting of KH_2PO_4, $Ca(NO_3)_2$, and $MgSo_4$, corresponding in molecular proportions to solution R_4S_1 of the National Research Council bulletin on "A plan for co-operative research on salt requirements of representative agricultural plants." Iron was added in the form of ferric phosphate in the concentation of approximately 3 p.p.m. Three concentrations of solution were used: 1., .1, and .01 atmospheres and renewed at intervals of four days during the growing period to prevent any great change in concentration due to salt absorption by the roots.

The seedlings were grown in four light intensities, obtained by use of electric lights and corresponding to 130, 70, 48, and 31 foot-candles as measured by the Macbeth illuminometer. Previous experimentation had shown that minimum light intensity for growth was approximately 50 foot-candles, with continuous illumination. Temperature was kept at 70 degrees Fahrenheit, with a maximum variation of about 2 degrees. Relative humidity was maintained at 80 per cent with a range of fluctuation of about 10 per cent.

Records were kept of the amount of solution used in transpiration in the different intensities and concentrations of solution. At the end of a

[31] Lundegardh, Henrik. Klima und Boden in ihrer Wirkung auf das Pflanzenleben. Jena (1925).

TABLE IV

Light Intensity in Ft.-Cndls.	Conc. Sol. in Atm.	Gain Dry Wt.* in Grams.	Gain in Length** in mm.	
			Tops	Roots
130	1.0	3.20	65	218
130	.1	3.27	72	150
130	.01	2.43	61	131
70	1.0	1.70	39	175
70	.1	1.74	51	119
70	.01	1.50	49	117
48	1.0	.84	53	120
48	.1	.86	58	107
48	.01	.77	51	100

* Average of 24 individuals.
** Average of 39 individuals.

ten-week growing period the seedlings were removed from the jars and studied for gain in dry weight, length of roots and stems, and general vigor. The data so obtained is summarized in Table IV. It covers only the seedlings grown in the three higher light intensities since the plants

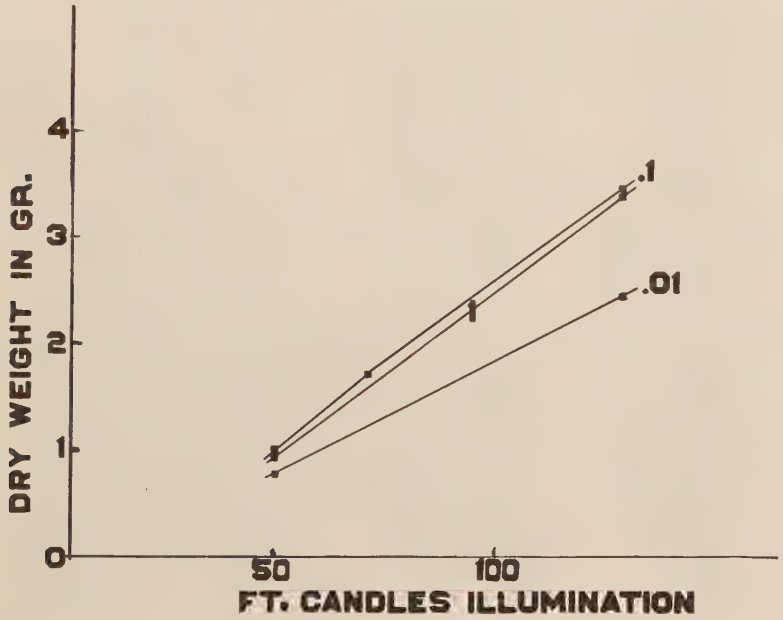

FIG. 9. Graph showing relation between intensity of illumination and gain in dry weight.

TABLE V

Light Intensity in Foot-Candles	Conc. of Sol. in Atm.	Grs. Water Transpired Grams Dry Material
130	1.	370.4
130	.1	439.4
130	.01	374.5
70	.1	498.1
48	1.	583.9
48	.1	971.6
48	.01	843.2

FIG. 10. Photograph showing differences in root development brought about by varying the concentration of the nutrient solution.

grown in the lowest light intensity did not survive more than one or two weeks and showed no evidence of growth during that period.

The influence of concentration of solution on gain in dry weight in the different light intensities is shown graphically in Fig. 9. There appeared to be no significant differences between the gain in weight in solutions of 1 and .1 atm. concentration. The solution of .01 atmosphere concentration appeared inadequate for growth in all light intensities. The most marked difference between the effects of the higher concentrations on growth appeared in root and top development. These differences are shown in Fig. 10. Taken as a whole the solution of .1 atmosphere concentration appeared most favorable for growth. Although there was a great increase in length of the roots of plants grown in solution of 1 atmosphere concentration over those grown in the .1 atmosphere solution this was offset by a general lack of branching and development of side roots.

Summary

1. Previous work on certain aspects of light as a factor in plant growth is reviewed.

2. A method is described for the determination of spectral quality of forest light with a portable spectrophotometer and a method of differentiating between the different sources of light.

3. Results are given of an analysis of different types of shade in the forest with particular reference to direction and quality of light and factors influencing the same.

4. Shade or reduced light intensity in the forest is subdivided into three types, depending upon whether or not the light is diffused sky light. Different types of forest canopy are discussed in relation to transmission and reflection of light by foliage leaves.

5. Differences in opinion regarding composition of forest light are explained on the basis of data presented in the present paper.

6. Tree seedlings grown under controlled conditions of light intensity, temperature, and relative humidity but subjected to different concentrations of nutrient solution were studied for increase in dry weight and development of roots and tops. The results do not indicate that a higher concentration of available nutrients increases the ability of seedlings to endure a high degree of shading. The data indicate the necessity of controlling the concentration of mineral nutrients in determining the effects of light on growth and development.

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